STUDIES ON THE PHYSIOLOGICAL VARIATION BETWEEN TROPICAL AND TEMPERATE ZONE FIDDLER CRABS OF THE GENUS UCA. II. OXYGEN CONSUMPTION OF WHOLE ORGANISMS [1]

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The year 1936 marked a new era in investigating compensatory adaptation of the rate of metabolism in organisms from different latitudes. In this year Sparck, Thorson, and Fox independently reported on intra- and interspecific differences in rate functions of organisms in Greenland, the North Sea, and the Mediterranean Sea. Since then a number of other papers dealing with this subject have appeared and recently Prosser (1955) and Bullock (1955) reviewed this area of study.

Studies of the physiological variation of latitudinally isolated populations of fiddler crabs, genus *Uca,* were undertaken to determine the extent of this variation and to correlate these results with their distribution. The first paper in this series (Vernberg and Tashian, 1959) dealt with a study of the thermal death limits of tropical and temperate zone animals as affected by thermal acclimation. The present paper reports on their rate of oxygen consumption as influenced by starvation, size, season and temperature. Although it may be a question as to what constitutes a valid measure of climatic adaptation, it was felt that the rate of oxygen uptake would reflect changes in the physiological response of a total organism more nearly than studies involving its component parts. Subsequent studies will deal with differences in tissue and enzyme activity in respect to climatic adaptation.

Rather than attempt to review all the literature relating to this general problem, the present paper will be restricted to those papers pertaining to oxygen consumption.

Thorson (1936), comparing metabolic rates of lamellibranchs from Greenland and the Mediterranean, reported the following general facts (p. 121): "Hence it would seem that species with a northerly distribution have a higher metabolism than southerly distributed species of the same genus at the same temperature. . . ." He also found a close correlation between oxygen consumption and habits of animals, in that epifaunal forms have a comparatively higher metabolic rate than digging species and level-bottom species. In addition, he noted that certain arctic

species are very sensitive to slight increases in temperature. Also working with lamellibranchs, Sparck (1936) obtained similar results.

The work of Fox and subsequent papers in collaboration with Wingfield cite further evidence relating to this problem. When comparing metabolic rates of pairs of marine organisms from Kristineberg, Sweden and Plymouth, England, Fox (1936) found the reverse metabolic-temperature response reported by Thorson and Sparck, *i.e.*, the rates of the warmer-water species were higher than their Swedish counterparts when measured at the normal temperature at which the species were collected. However, he reported that the rate of respiratory movements of southern forms at 16.5° C. was the same as northern forms at 5.5°. In 1937 Fox and Wingfield, studying two additional species, one from northern waters and the other one from more southern waters, observed that the metabolic-temperature curves obtained for whole animals and isolated muscle tissue were parallel. They concluded that the greater rate of oxygen consumption of warm water animals is due to greater non-locomotory metabolism. However, in later papers by Fox (1939) and Wingfield (1939), they stressed that when taking into consideration such factors as body size and season aquatic poikilotherms from the north usually will exhibit a higher rate of physiological function at a given temperature than their more southern relatives. Later Berg (1953) reviewed these results of Fox and Wingfield and concluded that most of the exceptions cited by them actually showed some degree of acclimation.

In 1953 Scholander *et al.* measured the rate of oxygen consumption at various temperatures of 38 species of tropical and arctic poikilotherms, including fishes, crustaceans, insects and spiders. They concluded that there is considerable, but incomplete, metabolic adaptation in aquatic arctic forms relative to aquatic tropical species, while terrestrial insects revealed slight adaptation if at all. (They were of the opinion that no evidence has been found to show that organisms are adapted to temperate fluctuation by being metabolically insensitive to temperature changes.)

Reporting on metabolic rates of the two sub-species of *Uca pugnax* from Trinidad, B.W.I., Florida, North Carolina and New York, Tashian (1956) found marked differences in the response of species from the tropical and temperate zone. Recently Tashian and Vernberg (1958) have elevated these sub-species to the specific level. Data on oxygen uptake of latitudinally isolated populations of *Uca pugilator* have been reported by Edwards (1950) and Démeusy (1957). Roberts (1957a, 1957b) studied the shore crab, *Pachygrapsus crassipes*, from different localities on the west coast of California and Oregon and reported a difference in the resting metabolism which could be attributed to compensation for local temperatures. Results of the present paper, while further substantiating some of the findings of the above workers, also breach the gap between some apparent differences reported by various investigators.

Material and Methods

Fiddler crabs are an excellent group of animals to study as they are abundant over most of the eastern coastline of the Americas and islands of the Caribbean (Rathbun, 1918). The various species have either temperate zone or tropical zone affinities, and, in addition, there is an area of overlap of some northern and

some southern forms along the northeast coast of Florida (Tashian and Vernberg, 1958).

Animals used in this study were collected from the following areas: Beaufort, North Carolina, latitude 35°; Alligator Harbor, Florida, latitude 30°; and Jamaica, West Indies, latitude 18°. Experimental studies on fiddler crabs from North Carolina and Florida were conducted either at the Duke University Marine Laboratory or at Duke University, and tropical species were studied at the University College of the West Indies, Jamaica. The following is a brief description of the range and local distribution of the seven species of *Uca* used in this study.

Uca minax (Le Conte). Ranges from Massachusetts to Texas (Rathbun, 1918). In the region of Beaufort, North Carolina this species is typically found in the section of the *Spartina* marsh which is farthest from the banks of the drainage ditches and immediately preceding the *Salicornia-Distichlis* zone.

Uca pugilator (Bosc). Ranges from Massachusetts to Texas (Rathbun, 1918). Usually this species is associated with the sandy-muddy beaches of either the protected areas of the harbor or along the sandy sections of the salt marshes.

Uca pugnax (Smith). Ranges from Massachusetts to northeast Florida (Tashian and Vernberg, 1958). Locally this species is found on mud flats along with *U. pugilator* or in muddy areas of the *Spartina* marsh.

Uca rapax (Smith). Ranges from northeast Florida to Brazil (Tashian and Vernberg, 1958; de Oliveira, 1939). In Florida this species may be found alongside *U. pugnax* or more generally nearer the high tide level in sandy soil. In Jamaica this species was collected in many habitats ranging from sandy soils to mangrove swamps.

Uca mordax (Smith). Ranges from the Bahamas and the Gulf of Mexico to Brazil (Rathbun, 1918). In Jamaica this species was frequently collected on sandy-clay flats and among mangrove roots.

Uca thayeri (Rathbun). Ranges from northeast Florida to Brazil. This species was abundant in muddy banks of drainage ditches where *U. rapax* were frequently caught.

Uca leptodactyla (Rathbun). Found from the west coast of Florida and the Bahamas to Brazil (Rathbun, 1918). A small-sized species which was found only on protected sandy-mud beaches.

The three species of fiddler crabs studied from North Carolina were *Uca minax*, *Uca pugnax* and *Uca pugilator*. In Jamaica, determinations were made on *U. leptodactyla, U. rapax, U. mordax* and *U. thayeri*. *U. rapax* and *U. mordax* came from the Port Henderson area, while *U. leptodactyla* were collected from the swamp near the Morant Point Lighthouse, and *U. thayeri* from Port Morant. Only *U. rapax* were studied from Alligator Harbor, Florida.

After collecting the animals and bringing them to the laboratory, they were rinsed in sea water and placed in aquaria containing about one-half inch of sea water. Animals kept as a general supply were exposed to hamburger, fish and Pablum once or twice a week for about 12 hours and then the sea water was changed. Most of the animals appeared to be feeding and in a good state of nutrition as fecal pellets were readily observed and mortality was low. Individuals to be used experimentally were isolated in marked glass containers and then subjected to the condition of the experiment.

Oxygen consumption was determined by means of standard manometric techniques (Umbreit, 1957). A large-sized respirometer flask (volume about 125 cc.) was connected to a conventional Warburg manometer for all determinations, except in the series of experiments involving the smallest sized species, *U. leptodactyla,* where a flask with a volume of 8 cc. proved to be better. A measured amount of filtered sea water was introduced into a flask containing an organism. The salinity was not measured each time but sporadic measurements gave values ranging from 31 to 35 0/00. In all cases a determination of the rate of oxygen consumption involved only one organism per flask. Ten per cent KOH was used to absorb CO_2. Flasks were not shaken as this understandably proved to be too excitatory to the animals. All results are expressed as μl. oxygen consumed/minute/gram of wet weight. Determinations of oxygen consumption were made over a graded temperature series by the use of a thermally controlled water bath. Preliminary studies showed that the time interval required for thermal equilibration and for the rate of oxygen uptake to reach a somewhat steady level varied inversely with temperature. Only oxygen consumption data which were relatively stable over a period of time were used. The duration of the experiment also varied with temperature: at high temperatures rates were determined over a two-hour period, while at low temperatures eight hours of observation were used.

Recent workers have reported on cycles of oxygen consumption in fiddler crabs which were correlated with time of day, tide, seasons, and other factors (Edwards, 1950, and Brown *et al.,* 1954). In the present study an attempt was made to minimize variation due to rhythmic daily fluctuations by making an equal number of determinations in the afternoon and the morning. It is interesting to note that a preliminary study comparing determinations made on the same animals run in the morning and afternoon did not show any consistent variation. Although no attempt was made to correct for possible tidal influence on metabolism, seasonal variation was observed in some species and this will be discussed later.

The recent thermal history of animals from North Carolina and Jamaica was the same in that their habitat and laboratory temperatures were alike, although the determinations were made at different times of the year. The mean water temperature at Jamaica varies slightly throughout the year, ranging from 80°–82° F. while the range during June–August in the Beaufort area was from 77°–82° F. Work at Beaufort extended from June to September, while studies in Jamaica began in October, 1957, and ended in April, 1958.

In all of these studies only male crabs in the intermolt stage were measured. The criteria of Drach (1939) and Guyselman (1953) were used to determine the stage of the molting cycle.

When oxygen consumption data were plotted on logarithmic co-ordinates with rate of oxygen uptake (weight-specific) against the weight of the organism, a regression equation was obtained of the type

$$\frac{O_2}{W} = aW^{(b-1)},$$

where O_2 is oxygen consumption/unit time, W the body weight (wet weight), and a and b are constants, indicating the intercept and the slope of the regression line in the log-log plot. Additional statistics calculated were the standard error, $S(\log y. \log x)$, and coefficient of correlation (r).

Experiments and Results

Influence of starvation on metabolism

One variable in comparing metabolic rates of animals is the degree of starvation. To determine variation due to this factor, 25 specimens of *U. pugnax* from North Carolina were collected, isolated individually, and maintained at room temperature. First, their rate oxygen consumption was determined after being exposed to food and subsequently determined after the first, third, fifth, seventh, ninth, sixteenth and twenty-first day of starvation. Of the original 25 animals, 21 survived for the entire period while four animals died after the sixteenth day. Results represented in Figure 1 are averages of the 21 animals surviving the entire 21 days of starvation.
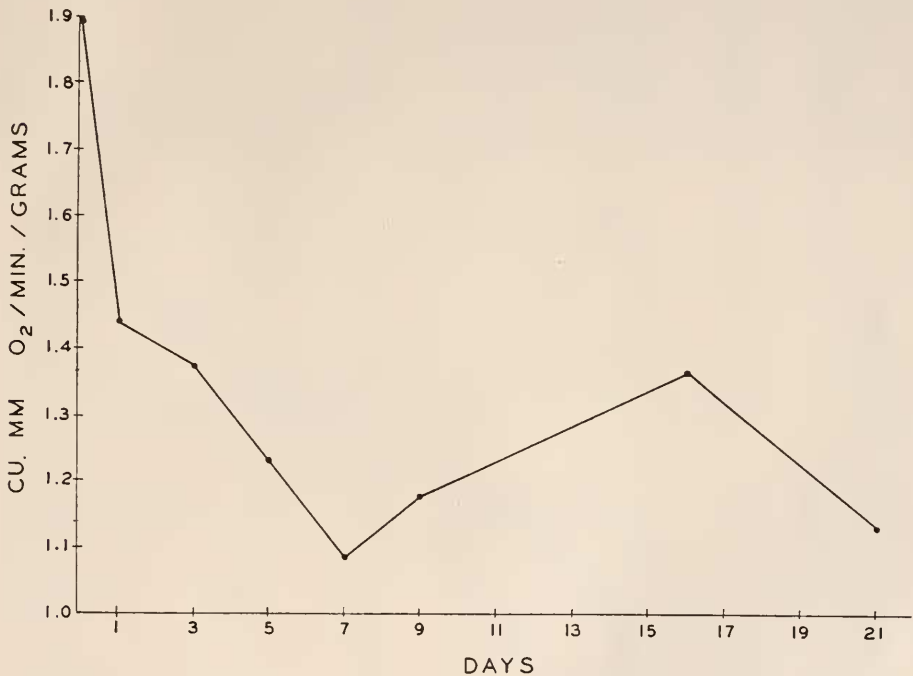

FIGURE 1. The influence of starvation on the rate of oxygen consumption of *Uca pugnax*. Determinations made at 28° C.

A marked drop occurred by day 1 followed by a progressive decline in metabolic rate and subsequent insignificant fluctuations. On the basis of these findings, animals were starved for one to three days before being used in any experiment unless otherwise specified.

The response pattern to starvation of *U. pugnax* is similar to results observed in *Pachygrapsus crassipes* (Roberts, 1957a), pulmonate snails (von Brand, Nolan and Mann, 1948) and fish (Wells, 1935).

Metabolic rates of tropical and temperate zone Uca

Table I represents the rates of oxygen consumption of seven species of fiddler crabs from the tropical and temperate zones determined at different temperatures. Although an increase in temperature generally resulted in a higher rate of oxygen uptake, there appear to be certain thermal ranges within which the metabolic rate is little influenced.   A specific example can be seen for *U. pugnax* in that the rate of oxygen consumption at 7° and 12° is similar, but a sharp increase followed when determined at 17°.   Throughout the temperature range of 12°–17° (determinations made at 12°, 15°, and 17°), *U. pugilator* and *U. minax* consumed oxygen at about the same rate (Fig. 2).   This phenomenon was observed at higher temperature ranges as well for these temperate zone animals; for example, a five-degree increase from 28°–33° only slightly increased the metabolic rate of *U. minax*.   This apparent "staircase" effect was noted for tropical animals also, but only at the intermediate and higher temperature levels (Fig. 3).

Changes in the rate of oxygen consumption are expressed as Q_{10}, according to Van't Hoff's equation, rather than the heat of activation (*u*) of Arrhenius. Q_{10} values for these seven species found in Table II further help to illustrate this "staircase" phenomenon.   If determinations had been made only at larger thermal
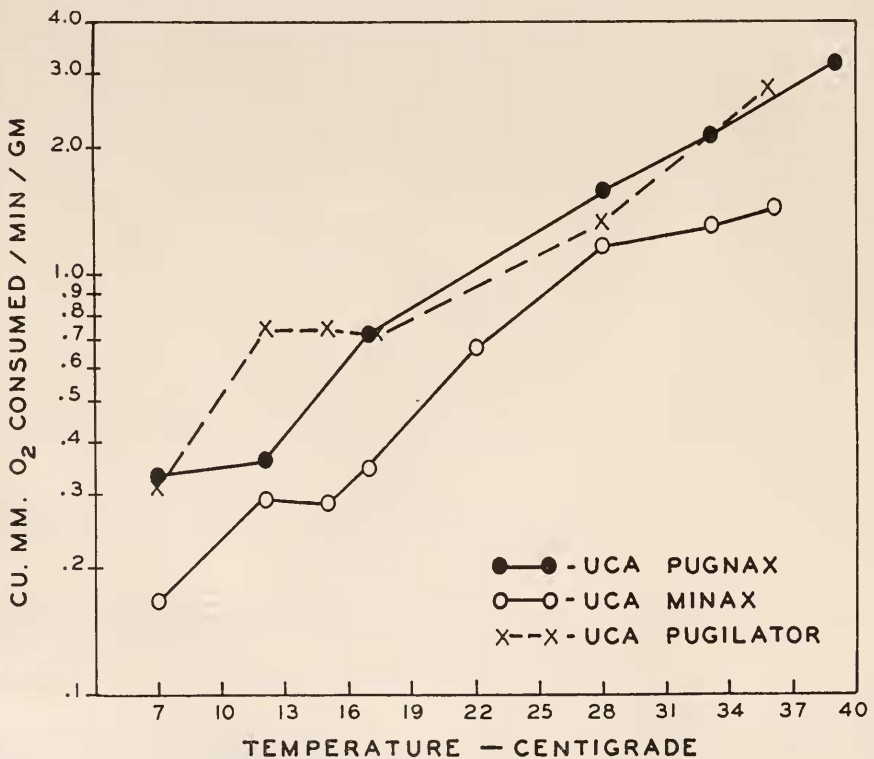

FIGURE 2.   The influence of temperature on the rate of oxygen consumption of three species of *Uca* from North Carolina.

TABLE I

Rate of oxygen consumption of Uca from the tropical and temperate zones determined at various temperatures

| Species	Temperature (° C.)	Size of sample	Body weight (gms.)		Rate of O₂ consumption (mm.³/min./gram)	
			Mean	Range	Mean	Range
pugnax	7	19	2.57	0.94– 4.72	0.328	0.156–0.725
	12	33	2.70	1.06– 4.65	0.357	0.179–0.730
	17	31	3.63	0.88– 5.95	0.734	0.296–1.410
	28	54	2.90	1.15– 5.57	1.587	0.485–3.489
	33	19	2.95	0.65– 4.31	2.140	1.131–3.705
	39	18	3.20	0.89– 5.57	3.278	2.020–4.523
minax	7	17	6.19	3.85– 8.56	0.167	0.109–0.280
	12	25	6.57	4.54– 9.05	0.292	0.135–0.622
	15	26	6.48	4.79– 8.94	0.281	0.129–0.567
	17	26	6.44	4.58– 8.61	0.342	0.133–0.689
	22	24	6.33	4.41– 8.83	0.688	0.350–1.207
	28	66	5.77	1.66– 8.42	1.185	0.566–2.554
	33	23	6.61	5.04– 8.28	1.308	0.841–1.751
	36	22	6.60	5.01– 8.06	1.442	0.915–1.907
pugilator	7	17	2.06	0.89– 2.84	0.311	0.122–0.627
	12	13	2.03	0.62– 2.95	0.751	0.412–1.482
	15	22	1.87	0.68– 2.95	0.757	0.379–1.395
	17	23	1.93	0.66– 3.41	0.723	0.426–1.264
	28	63	2.35	0.95– 4.87	1.333	0.806–2.473
	36	17	2.06	0.93– 3.00	2.729	1.962–3.896
rapax from Florida	7	24	2.80	1.42– 5.12	0.352	0.150–0.553
	12	32	2.60	1.25– 5.12	0.732	0.280–1.561
	17	30	2.51	1.25– 5.12	1.017	0.396–2.048
	27	97	1.82	0.95– 5.12	2.109	1.125–3.802
	33	13	3.17	1.66– 5.12	2.324	1.558–3.332
	36	25	2.00	1.00– 5.12	2.838	1.315–6.042
rapax from Jamaica	12	25	3.78	0.57– 9.33	0.349	0.167–0.525
	15	40	4.36	0.63–11.57	0.665	0.272–1.877
	17	29	3.51	0.67– 9.33	0.958	0.327–1.931
	22	24	3.10	0.84– 6.56	1.468	0.746–2.369
	28	54	4.33	0.58–13.67	1.663	0.641–4.139
	33	26	3.69	0.67– 9.54	1.954	0.890–3.304
	36	26	3.36	0.58–13.67	2.400	0.801–4.597
	39	23	4.65	0.92–13.67	2.807	0.683–4.497
thayeri	12	11	4.38	1.50– 6.51	0.240	0.149–0.333
	15	12	5.25	2.71– 7.96	0.528	0.383–0.859
	30	13	4.36	2.71– 6.51	1.412	0.675–1.980
	36	16	4.60	1.65– 8.74	1.838	1.306–2.471
mordax	12	9	2.81	1.53– 3.84	0.392	0.216–0.548
	15	7	2.41	0.91– 3.63	0.582	0.462–0.713
	22	8	2.50	0.91– 4.26	1.436	0.884–2.023
	28	12	2.67	0.87– 4.28	1.603	0.942–2.835
	36	11	2.49	0.87– 4.24	2.885	1.457–4.460
leptodactyla	12	11	0.26	0.15 0.31	0.294	0.115–0.545
	15	13	0.28	0.18– 0.35	0.674	0.460–1.176
	30	14	0.27	0.18– 0.36	2.495	1.748–3.768
	36	13	0.28	0.19– 0.35	3.842	2.588–4.973
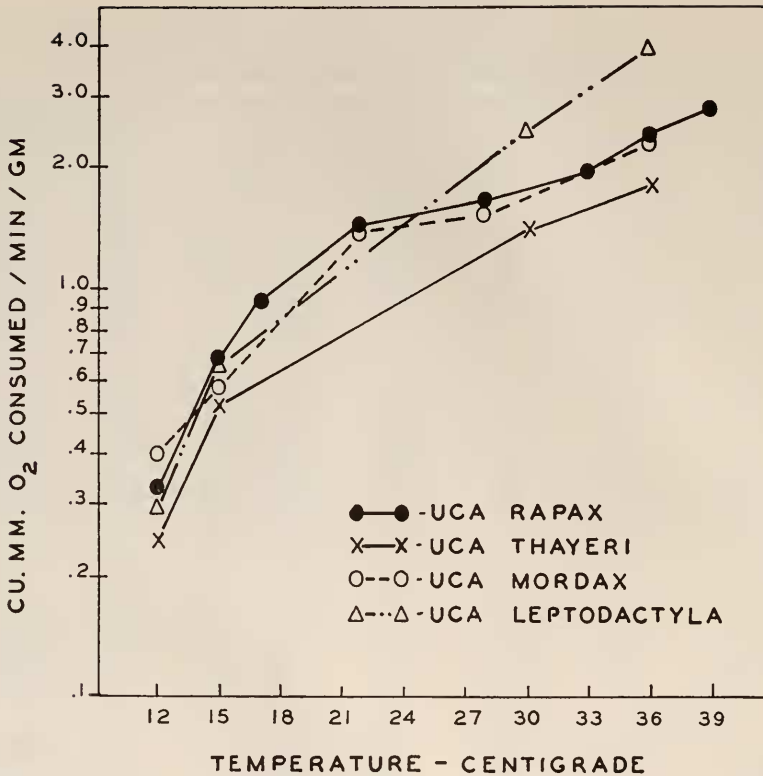
FIGURE 3. The influence of temperature on the rate of oxygen consumption of four species of *Uca* from Jamaica, The West Indies.

intervals, for example every 10 degrees, this type of response would not have been very evident. The Q_{10} value for *U. pugilator* for the temperature range of 7°–17° was 2.32 while a value of 5.83 was obtained for the range of 7°–12°. Tropical species afford additional examples; *U. rapax* had an exceptionally high Q_{10} value of 8.58 over a three-degree increase from 12°–15°, whereas a Q_{10} value of 4.20 for the 10-degree range of 12°–22° was observed.

In general lower Q_{10} values were obtained at higher temperatures than at lower temperatures for all seven species of *Uca* examined. A marked difference in metabolic behavior between tropical and temperate zone animals was observed at the lower temperatures. Between 12° and 15° very high Q_{10} values were obtained for *U. rapax, U. leptodactyla* and *U. thayeri* (range from 8.58–15.9) while a moderately high value of 3.73 was observed for *U. mordax.* Although *U. minax* and *U. pugilator,* both temperate zone forms, showed no increase in metabolic rate within this same three-degree range, moderately high Q_{10} values were obtained between the 7° to 12° range. Determinations made at lower temperatures would probably result in still higher Q_{10} values for these two forms and also for *U. pugnax.* Thus it would seem that at certain points along a temperature gradient, a slight

TABLE II

Q$_{10}$ of oxygen consumption of seven species of Uca from tropical and temperate zones

Temperature range (° C.)	minax	pugnax	pugilator	rapax (Florida)	rapax (Jamaica)	mordax	lepto-dactyla	thayeri
7–12	3.06	1.20	5.83	4.36	—	—	—	—
7–17	2.04	2.24	2.32	2.89	—	—	—	—
7–28*	2.54	2.10	2.00	2.45	—	—	—	—
7–36	2.10	—	2.11	2.07	—	—	—	—
12–15	1.00	—	1.00	—	8.58	3.73	15.9	13.7
12–17	1.37	4.23	1.00	1.93	—	—	—	—
12–22	—	—	—	—	4.20	3.66	—	—
12–28*	2.40	2.51	1.43	2.02	2.65	2.41	3.28	2.67
12–36	1.95	—	1.71	1.76	2.23	2.27	2.92	2.33
15–17	2.67	—	1.00	—	6.20	—	—	—
15–22	—	—	—	—	3.10	3.49	—	—
15–28*	2.51	—	1.55	—	2.02	2.18	2.39	1.92
15–36	2.18	—	1.84	—	1.84	2.12	2.29	1.68
17–22	4.04	—	—	—	2.35	—	—	—
17–28*	3.09	1.97	1.75	1.86	1.63	—	—	—
17–36	2.45	—	2.01	1.71	1.62	—	—	—
22–28*	2.57	—	—	—	1.23	1.32	—	—
22–33	1.90	—	—	—	1.29	—	—	—
28–33*	1.22	1.90	—	1.42	1.38	—	—	—
28–36*	1.28	—	2.46	1.33	1.57	2.03	2.05	1.55
33–36	2.49	—	—	2.22	1.98	—	—	—

* Determinations were made at 27° for *rapax* (Florida) and 30° for *leptodactyla* and *thayeri*.

increase in temperature results in a marked increase in metabolic rate, whereas at other points the rate of oxygen consumption of these animals is relatively temperature-independent throughout a wider temperature range. Both temperate and tropical species exhibit this type of metabolic response but at different points on the temperature spectrum: tropical animals were metabolically activated at higher temperatures than temperate zone forms.

The similar Q_{10} values for both temperate and tropical zone animals obtained at intermediate and higher temperatures are not surprising as the recent thermal history of all seven species was very similar and reflected summer or elevated temperature conditions. However, at lower temperatures, tropical animals exhibit a reduced ability to meet metabolically this environmental stress, while temperate zone forms appear to be more labile.

When comparing the metabolism of tropical and temperate zone fiddler crabs over a wide range of temperatures, some rather interesting points can be noted. At 12° the range of the average rates of oxygen consumption of the four tropical species is from 0.240 to 0.392 while the range for temperate zone forms is 0.292 to 0.751. These figures would suggest that at this particular low temperature northern species tend to have higher metabolic rates. However, as will be discussed in more detail, it is necessary to take into consideration the factor of body size when comparing species. The following comparisons are of similar sized species: *pugnax-rapax-mordax* and *minax-thayeri*. At 12° *U. pugnax* from North Carolina and *U. rapax* and *U. mordax* from Jamaica consume oxygen at a similar

F. JOHN VERNBERG

TABLE III

Statistical analysis of relation of oxygen consumption to body size of Uca pugnax and Uca rapax determined at various temperatures

Temperature (° C.)	No. of determinations	b-1	$\log a$	$S_{\log y \cdot \log z}$	r
Uca rapax from Jamaica					
12	25	−0.377	−0.301	0.113	0.81
15	40	−0.236	−0.076	0.143	0.42
17	29	−0.571	0.192	0.139	0.75
22	24	−0.387	0.309	0.075	0.82
28	54	−0.343	0.360	0.146	0.64
33	26	−0.377	0.434	0.136	0.67
36	26	−0.374	0.498	0.135	0.77
39	23	−0.354	0.620	0.143	0.69
Uca rapax from Florida					
7	24	−0.050	−0.446	0.133	0.00
12	32	−0.474	−0.010	0.209	0.38
17	30	−0.465	0.150	0.161	0.29
27	97	−0.210	0.356	0.119	0.25
33	13	−0.456	0.574	0.076	0.65
36	25	−0.380	0.557	0.185	0.52
Uca pugnax from North Carolina					
7	19	−0.770	−0.234	0.094	0.88
12	33	−0.537	−0.266	0.102	0.63
17	31	−0.309	−0.003	0.162	0.36
28	54	−0.373	0.321	0.172	0.37
33	19	−0.304	0.423	0.158	0.44
39	18	−0.316	0.650	0.069	0.52

rate, while *U. pugilator* from North Carolina, with a weight average slightly less than these three species, consumed almost twice as much oxygen per unit weight and time. *U. minax*, another northern species, has a higher metabolic rate than *U. thayeri*. Oddly, *U. leptodactyla*, a very small tropical species, consumed oxygen at a rate similar to the larger sized species, while at elevated temperatures (30° and 36°) it had the highest metabolic rate of all seven species.

Determinations were not made at 7° on tropical species as it has been shown by Vernberg and Tashian (1959) that these animals are not able to withstand this low temperature for a long enough period: 50% mortality occurred after exposure to 7° for 30–40 minutes.

As noted above the oxygen consumption rate of tropical species was greatly increased by a three-degree increase from 12°–15° while temperate zone species are little affected.

At 28° *U. pugnax, U. mordax* and *U. rapax* again have similar metabolic rates, while values for *U. thayeri* are now higher than *U. minax* which is the reverse of
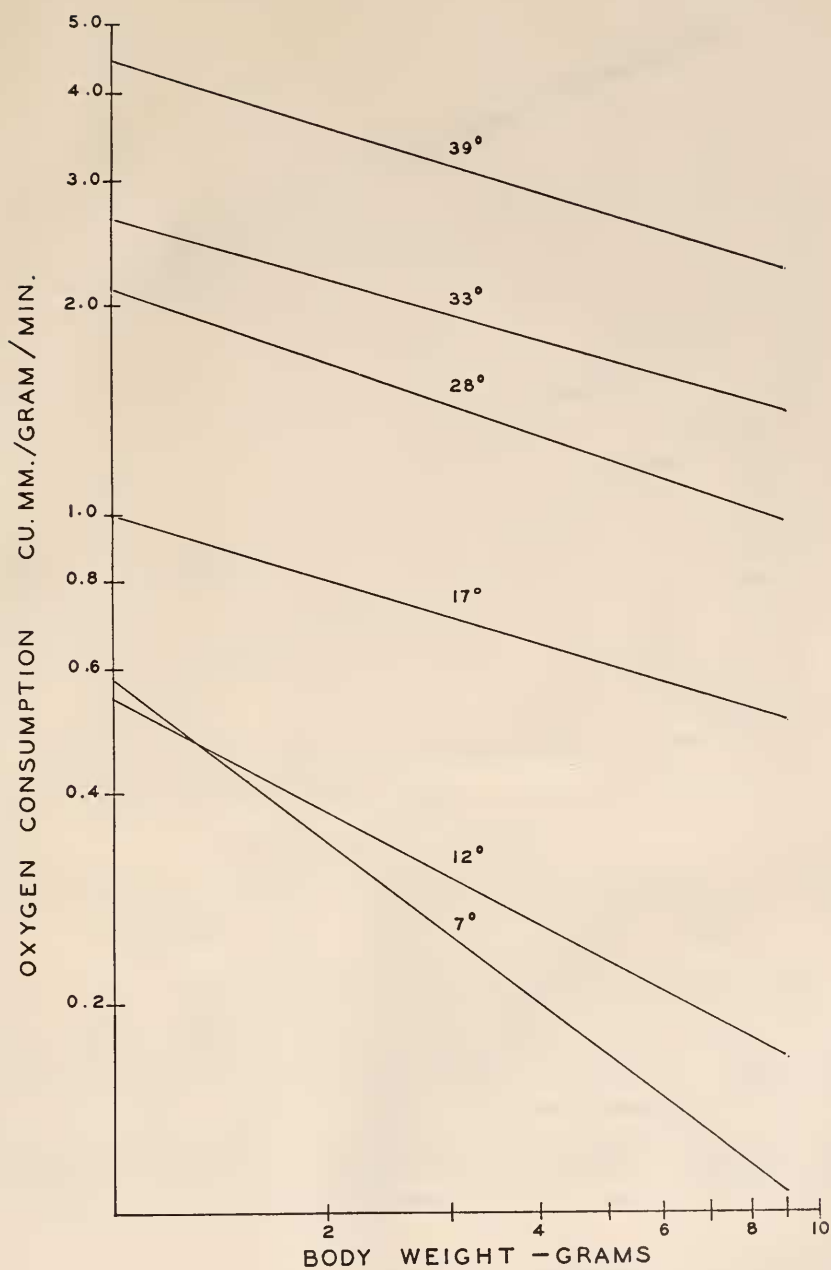
FIGURE 4. The relation of oxygen consumption to size in *Uca pugnax* from North Carolina when determined at different temperatures.
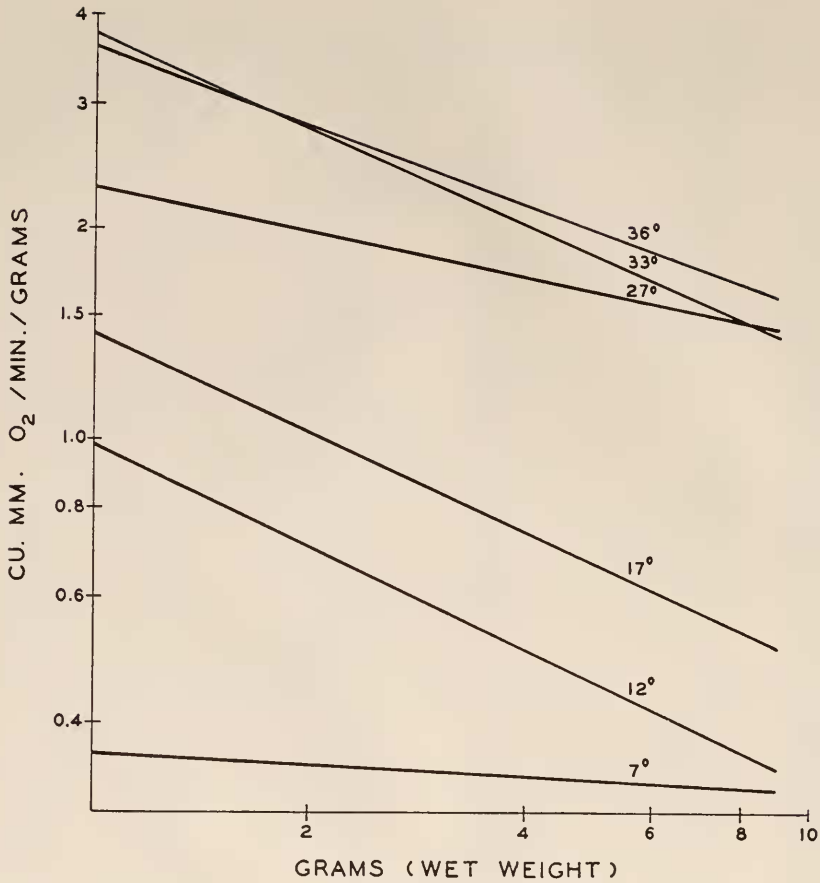
FIGURE 5. The relation of oxygen consumption to size in *Uca rapax* from Alligator Harbor, Florida when determined at different temperatures.

the results obtained at 12°. Although the temperate zone species *U. pugnax* utilized more oxygen than *U. rapax* at 33° and 39°, the tropical species *U. thayeri* consumed oxygen at a faster rate than *U. minax* at elevated temperatures. It would appear that no uniform metabolic difference between tropical and temperate zone species was apparent under the conditions of this study. At any temperature point one tropical species may consume oxygen at a faster rate than a similar sized northern organism, while at this same temperature a temperate zone species of another paired comparison would utilize oxygen faster than its tropical counterpart.

Influence of size on metabolism

Numerous workers have stressed the importance of the dependence of metabolism on body size when making inter- and intraspecific comparisons of crustaceans (Weymouth *et al.*, 1944; Vernberg, 1956; Tashian, 1956; Zeuthen, 1953; Roberts,
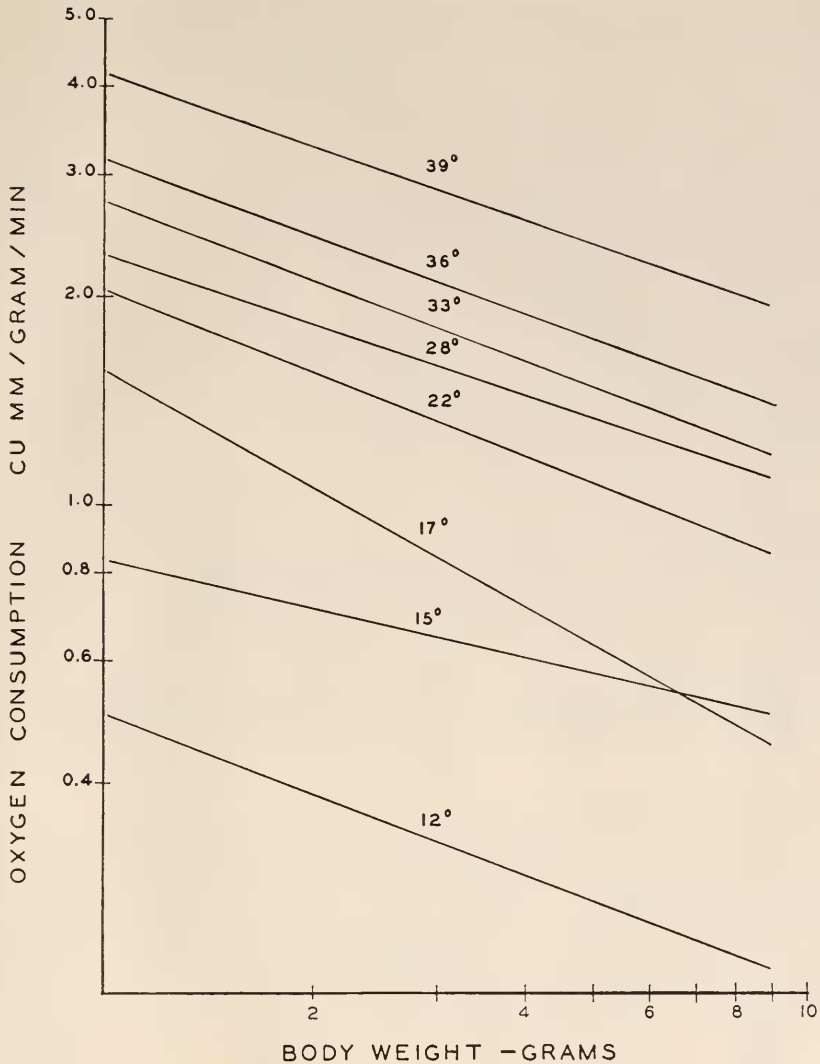
FIGURE 6. The relation of oxygen consumption to size in *Uca rapax* from Jamaica, The West Indies, when determined at different temperatures.

1957a; Edwards and Irving, 1943a, 1943b). In general, smaller individuals or smaller species consume oxygen at a faster rate per unit weight and unit time than larger individuals or larger species.

Oxygen consumption data determined at various temperatures were obtained using different sized animals of *U. pugnax* and two latitudinally separated populations of *U. rapax*. The comparative data for these two species, using the statistical techniques described earlier, are summarized in Table III. Figures 4, 5 and 6 represent the log-log plotting of the regression curves calculated from these data.

It appears that the slope of the regression curve varies with temperature. For *U. rapax* from Jamaica similar *b* values were obtained at all temperatures with the exception of 15°, where the slope was less steep, and 17° where the slope was steeper. The *b* constant for *U. pugnax* also fluctuated with the highest values, being obtained at low temperatures (7° and 12°). Oddly at 7°, *U. rapax* from Florida showed no correlation of body size and respiration, but at 12° the steepest slope was obtained. Although the absolute temperature at which the steepest slope was observed was different for these two species, it appeared that a significant break occurred at some low temperature. Interestingly this break occurred at a lower temperature for the northern species than for the tropical species. In general the slope of the regression curve was less steep for *U. pugnax* than *U. rapax*.

According to the method of Snedecor (1940, pp. 132–133), the correlation coefficients are significant at the 1% level for all points except for *U. pugnax* at 17°, 33°, and 39° where the level of significance is at the 5% level and *U. rapax* (Florida) at 7° where no significance was observed.

When the Q_{10} is calculated from the linear regression curves for animals weighing 1, 3.5 and 9 grams, an apparent difference in response correlated with body size is observed (Table IV). One size group may be more sensitive to a given temperature change than a different size group, *i.e.*, large specimens of *U. rapax* have a larger Q_{10} value than small sized (one gram) individuals at the temperature interval of 12°–15°, while at 15°–17° the reverse is observed.

After a log-log plotting of metabolic data of seven species of fiddler crabs obtained at two temperature levels, interspecific differences correlated with body size are evident (Fig. 7). At 28° or 30° a regression curve with a slope of − 0.204 was obtained which indicates that the small sized species consumes oxygen at a

TABLE IV

Q_{10} values of different sized Uca pugnax and Uca rapax based on linear regression curves

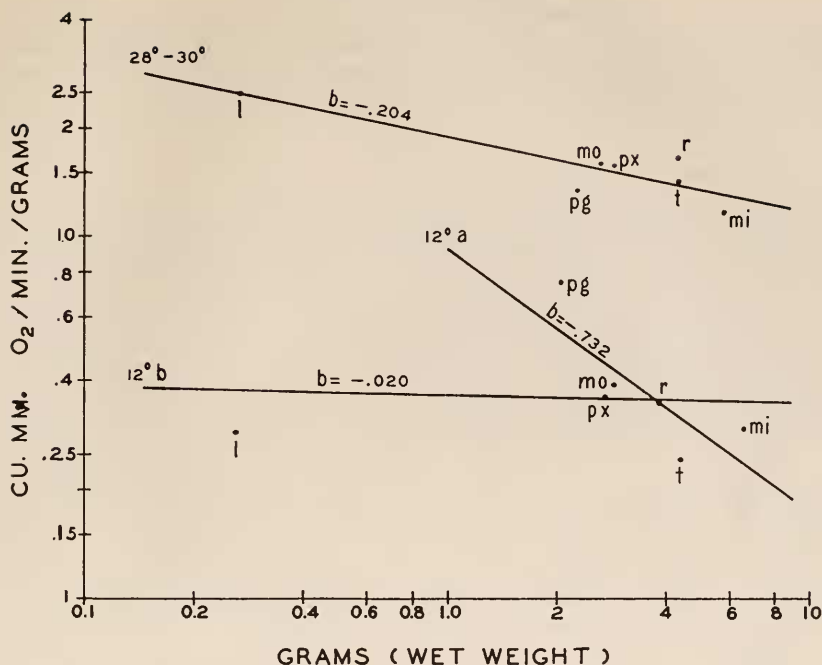| Temperature interval in ° C.	1 gram	3.5 grams	9 grams
Uca pugnax			
7–12	1.0	1.6	2.4
12–17	3.4	6.0	9.2
17–28	2.0	2.9	1.8
28–33	1.6	1.8	2.1
33–39	2.4	2.3	2.2
Uca rapax			
12–15	5.6	12.3	16.1
15–17	24.8	2.2	1.0
17–22	1.9	2.6	2.9
22–28	1.2	1.4	1.0
28–33	1.4	1.3	1.2
33–36	1.6	1.7	1.7
36–39	2.5	2.6	2.9

FIGURE 7. The relation of oxygen consumption to size in seven species of *Uca* measured at two temperature levels. Two regression curves were calculated for data at 12°: *a* did not include *leptodactyla* (1) whereas *b* did (see text for discussion). 1 is *leptodactyla*, mi is *minax*, mo is *mordax*, pg is *pugilator*, px is *pugnax*, ra is *rapax*, and t is *thayeri*.

higher rate than a larger sized species. However at 12° the metabolic rate of the small sized tropical species is greatly reduced in relation to the other six species and the regression curve has a slope of − 0.038 which is similar to results obtained for *U. rapax* (Florida) at low temperatures. But, if *U. leptodactyla* data are omitted on the basis of this tremendous response to environmental temperature stress, a curve with a slope of − 0.732 is obtained which seems to correspond to the steep slopes at low temperatures for intraspecific data on *U. pugnax* (a slope of − 0.770 at 7°) and *U. rapax* from Jamaica (a slope of − 0.571 at 17°).

Comparisons of metabolism of different populations of Uca rapax

Data on the oxygen consumption of *U. rapax* from Florida and Jamaica are included in Table I. One of the most obvious differences between the two populations is seen in their respective responses at reduced temperatures. The rate of oxygen uptake of Florida animals at 7° was very similar to that of Jamaican forms at 12°. As noted previously data for Jamaican animals at 7° could not be obtained as they did not survive exposure to this temperature. Following in this same trend, Florida animals consumed oxygen at a slightly higher average rate at 12° than their more tropical counterpart did at 15°. At all subsequent similar temperatures the subtropical form exhibited the highest metabolic rate.

U. rapax from Florida metabolically behaved like *U. pugnax* at the low temperature of 7° while at 12°, 17°, 27° and 33° *rapax* had a higher rate. The Floridan *U. rapax* exhibited the highest Q_{10} value at 7°–12° which is more characteristically like temperate zone forms than tropical zone species.

Influence of season on metabolism

Although results discussed up to this point were made on tropical and temperate zone animals which had similar recent thermal histories, experiments were carried out at different seasons of the year. Therefore the possibility of seasonal fluctuations in metabolism had to be investigated. Although metabolic studies involving Jamaican species were conducted from October to April, it was assumed that if any seasonal variation was to be observed it would be in evidence during this period as there is little monthly variation in temperature throughout the year.

When oxygen consumption determinations on *U. rapax* made either at 28° or 15° during October were compared with results of February–March, there was no significant difference of means. This indicated that under the conditions of these observations no shift in metabolism of *U. rapax* was observed which could be correlated with seasons (Table V).

Data on *U. pugnax* collected during the summer months and also during the period from November to January show a marked seasonal variation. At 7°, 17° and 28°, crabs collected during November and maintained in the laboratory under the same thermal conditions as summer animals (22°–27°) consumed oxygen at a significantly faster rate than summer animals run at the same temperatures. However, winter and summer animals responded similarly at 33°. The Q_{10} of 1.61 of "winter" animals was lower than that of summer animals (2.24) at low temperatures (7°–17°) but the opposite response was observed at higher temperatures (17°–28°) where the respective values were 2.37 and 1.97.

TABLE V

Metabolic rate of Uca pugnax determined at different seasons of the year and at various temperatures

Month of year	Temp. (° C.)	No. of determinations	Oxygen consumption rate (mm.³/ gm./min.)	Standard error of mean	Level of significant difference of means
June to August	7	19	0.328	0.035	>.01 highly significant
November to January	7	23	0.572	0.039	
June to August	17	31	0.734	0.047	>.01 highly significant
November to January	17	40	0.920	0.052	
June to August	28	54	1.587	0.094	>.01 highly significant
December to January	28	25	2.379	0.222	
June to August	33	19	2.140	0.207	no significant difference
December to January	33	27	2.312	0.113	

Discussion

Results of this investigation demonstrate the existence of differences in one physiological response, oxygen consumption rate, between temperate and tropical zone fiddler crabs. Other workers, using different measures of climatic adaptation, have reported the existence of physiological variation between latitudinally separated species of poikilotherms (Mayer, 1914, pulsation rate of the bell of *Aurelia aurita;* Hörstadius, 1925, Thorson, 1936, Moore, 1939, 1942, 1949, Dehnel, 1955, egg development and growth of various invertebrates and frogs; and Rao, 1953, rate of ciliary pumping of water in a mussel).

When making intra- or interspecific comparisons of poikilothermic animals from different latitudes, it is generally stated that at any given temperature, within limits a northern or cold-adapted form will show a higher metabolic rate than a southern or warm-adapted form. This comparison is dependent upon a number of other factors, such as body size and season, as pointed out so excellently by Prosser (1955), Bullock (1955) and Rao and Bullock (1954).

However, when comparing similar sized species of fiddler crabs from temperate and tropic zones, which have similar thermal histories, no consistent difference in metabolism correlated with latitude was observed except at low temperatures. But an intraspecific comparison of *Uca rapax* from northern Florida and Jamaica shows the classical type of response, especially at low and high temperatures. Using the data of Tashian (1956) it can be seen that similar sized fiddler crabs (3 gms.) from southern Florida and Trinidad had similar metabolic rates when determined at 24°, while the New York species was slightly lower. But at 14.1°–14.9° C., animals from New York weighing 3 gms. had a higher metabolic rate than the more southern forms. Working at still lower temperatures (1.4° and 15° C.) Démeusy (1957) reported that *Uca pugilator* from Woods Hole, Massachusetts had a significantly higher rate of metabolism than specimens from Florida only at the lower temperature. It is possible that these results might be influenced by seasonal temperature changes as this work was started in the fall. Whereas Démeusy did not find any difference at 15° between these two populations, Edwards (1950) reported the Woods Hole form of *U. pugilator* to have a higher rate of oxygen consumption at 20° than animals from Florida. No mention was made of either the thermal or seasonal history of the two populations studied. However, seasonal studies on *U. pugnax* indicated that "winter" animals from North Carolina had higher metabolic rates in the temperature range of 7°–25° than "summer" animals, while the tropical species, *U. rapax,* did not show any seasonal fluctuation. This absence of any seasonal variation in metabolism of *U. rapax* may be correlated with the thermal constancy of their environment throughout the year. However, fluctuating yearly temperatures of more northern latitudes have resulted in a labile metabolic pattern in *U. pugnax* which can be correlated with thermal acclimation.

Teal (1959), dealing with the relation of the respiratory metabolism of crabs to flow of energy through an ecosystem in Georgia salt marshes, found a marked ability of *U. pugnax* to demonstrate seasonal thermal acclimation.

The review paper of Bullock (1955) cites numerous examples of seasonal acclimation in many but not all poikilotherms. Recently Roberts (1957b) reported

that in the lined shore crab, *Pachygrapsus crassipes,* seasonal acclimation in metabolism was not present when determination was made at 16° C. However, he noted that respiration rates did bear some relationship to local seasonal temperature changes when intertidal sea water temperatures were below the environmental mean of 16°. It is noteworthy that the annual temperature flutuation experienced by *Pachygrapsus* is much less than that of fiddler crabs from North Carolina and thus might explain the difference in degree of response. The high and low mean monthly average temperature reported by Roberts was about 12° in January and 22° in August. At Beaufort McDougall (1943) and Gutsell (1930) reported similar average temperature values at 5.5° in February and 28° in July.

Metabolic rate determinations made at a number of temperature levels give a better insight into the influence of temperature on metabolism than generalizations from a few widely separated thermal points. The results of the present paper show that certain points along a temperature gradient appear to be of a more "critical" nature for the organism than others. This type of metabolic response when graphed gives a "staircase" appearance. In general tropical and temperate fiddler crabs responded similarly at intermediate and elevated temperatures, but at low temperatures tropical species were metabolically activated at a higher temperature than more northern species. Woodworth (1936) and Vernberg and Mariney (1957) observed that terrestrial insects, bees and fruit flies, respectively, were relatively temperature-insensitive within a given temperature range. Takatsuki (1928) showed a similar response in the heart rate at various temperatures of oysters from the tropical and temperate zone seas. When comparing the results of this study with those of Teal (1959), a remarkable similarity is observed. To cite a few examples: Teal observed *U. minax* consumed oxygen at the same rate at 11.1° as at 15.9°; in the present study the temperature range of 12° to 17° had little effect on their metabolism. *U. pugilator* was found to be temperature-insensitive between 13.2° and 19.4° by Teal and in the present investigation the same response was noted from 12° to 17°. Noteworthy is the similarity of the response of *U. pugnax.* In both studies, this species behaved differently than the other two species of *Uca:* while *pugilator* and *minax* were temperature-insensitive in this range of about 11°–19°, the metabolic rate of *pugnax* was greatly increased. Additional cases, chiefly terrestrial animals, are cited by Bullock (1955).

In general this marked influence of a relatively narrow temperature increase may be expressed in terms of a high Q_{10} (values greater than 3). After reviewing and re-evaluating many papers, Rao and Bullock (1954) concluded that Q_{10} was dependent on size and temperature of adaptation. Results of the present paper present additional data to show that marked differences in Q_{10} exist in the semi-terrestrial crabs of the genus *Uca* from the tropical and temperate zones. Scholander *et al.* (1953) measured the metabolic rate of *U. mordax* from Panama and reported high Q_{10}'s at low temperatures. However it is difficult to compare results for the following reasons: 1) determinations were made only at 10-degree intervals; 2) Q_{10}'s were estimated by eye-fitted tangents to eye-fitted curves; and 3) few data were available at 10°, as only three out of eight animals survived sufficiently long to give valid readings.

Similar results as the present paper were obtained by Thorson (1936), the

most striking example being a Q_{10} of 21 over the temperature range of $-1°$ to $1°$ for *Pecten groenlandicus*. Interestingly this lamellibranch lives in the fjords of Greenland where the temperature is constantly below $0°$. The same type of response appears in the results of Sparck (1936) but it is difficult to understand the basis of his metabolic-temperature curves as no experimental data are given and no points are shown on the curves. Démeusy (1957) and Teal (1959) observed a similar pattern of Q_{10} values with their work on *Uca*.

Results of the present paper demonstrate the dependence of metabolism on body size both when making inter- and intraspecific comparisons. The slope of the linear regression (b-1) varies with temperature: the steepest slope is at a higher temperature for the tropical species than for its northern counterpart. Although there are only a few observations, these results show the same tendency of temperature to influence metabolism as did Q_{10} values for the 7 species. Roberts (1957a) observed that the slope of the linear regression was the same at $8.5°$ and $16°$ for *Pachygrapsus* but was significantly less steep at $23.5°$. In their recent review paper, Rao and Bullock (1954) replotted the data of Edwards and Irving (1943a) and Edwards (1946) and found that the slope varied with temperature: 1) with summer animals, the slope was steeper at $12°$ than at $22°$; and 2) with winter animals the reverse was noted. As a consequence of the change in slope of the regression curve, the Q_{10} values of different sized organisms will be changed. Bishop (1950, p. 242) reported that smaller individuals of a species are more temperature-sensitive than larger ones, while Rao and Bullock (1954) concluded that commonly the Q_{10} increases along with increasing size within normal ranges of temperature. Results of the present paper show that the influence of temperature on the metabolism of different sized individuals of one species varied with the temperature range which was used. Therefore apparent differences reported in the literature may have resulted from comparing different temperature ranges of animals.

Interspecific comparisons of fiddler crabs showed the slope of the linear regression to be -0.204 at $28°$–$30°$ which compares favorably with slopes obtained for various groups of organisms (Zeuthen, 1953, -0.20 for crustaceans; Weymouth *et al.*, 1944, -0.174 for various crustaceans; and Vernberg and Hunter, 1959, -0.21 for cercariae of digenetic trematodes). But, when compared with the results at $12°$ C., marked differences are observed. The metabolic rate of the smallest species was depressed greatly by reduced temperature resulting in a regression slope of -0.020. Hence, smaller sized fiddler crabs have higher Q_{10}'s than larger sized species with the temperature range of $12°$ to $28°$ or $30°$.

Results of this paper would suggest that the metabolic response of fiddler crabs has real significance to their distribution. In the course of evolution, the various populations studied appear to be metabolically adjusted to the temperature fluctuations of their habitats. Temperate zone species not only are metabolically active at lower temperatures than tropical species but they exhibit a seasonal cycle as well. These differences are not only very marked when making interspecific comparisons but intraspecific differentiation is observed. The northernmost population of *U. rapax* behaves more like a temperate zone species at low temperatures than its southern relatives.

SUMMARY

1. The rate of oxygen consumption of seven species of *Uca* from the tropical and temperate zones was determined over a graded temperature series. All species had a similar recent thermal history.

2. Starvation resulted in an initial decrease in metabolic rate followed by a relatively constant rate in *Uca pugnax*.

3. Generally increased temperature resulted in increased rates of oxygen consumption. However, in some cases a given temperature range had little or no effect on metabolism, while at other temperatures a marked increase resulted.

4. Q_{10}'s of temperate and tropical zone species were similar at intermediate and higher temperatures but differed at lower thermal levels. Q_{10} varied with size and temperature levels. Lower Q_{10}'s were obtained at higer temperatures.

5. Intra- and interspecific comparisons of metabolism-size relationships were made on data obtained at various temperatures. The slopes of the regression varied with temperature and species.

6. When comparing the metabolic response of two latitudinally isolated populations of *Uca rapax* with a closely related temperate zone species, the pattern of the northernmost population of *U. rapax* was intermediate between the tropical and temperate zone forms.

7. Although no seasonal variation in metabolism was observed in tropical species, fluctuation was observed in a temperate zone species.

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